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Contrasting effects of altitude on species groups with different traits in a non-fragmented montane temperate forest

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Abstract

Temperature has strong effects on species composition and traits. These effects can differ within and between species groups. Thermoregulation and mobility are traits which can be strongly affected by altitudinal distribution. Our aim was to investigate the influence of altitude on the species richness, abundance and composition of species groups with different trophic, thermoregulatory and mobility traits. Carabids (Coleoptera; Carabidae), hoverflies (Diptera: Syrphidae) and birds (Aves: Passeriformes) were counted in three altitudinal belts with a total elevation difference of 700 m (from 300 m to 1000 m a.s.l.) in the same habitat type (non-fragmented temperate montane mixed beech and fir forest). We found that endotherms and more mobile species (i.e. birds) had a smaller turnover than ectotherms (i.e. hoverflies) and less mobile species (i.e. carabids), from which we can predict that the former species will undergo a less extreme shift than the latter in global warming scenarios. Species turnover across the altitudinal gradient increased from birds to hoverflies to carabid beetles. The effect of altitude on phenology was different between the studied ectotherm species groups (carabids and hoverflies). Hoverflies experience a phenological delay of species richness and abundance at higher altitudes in spring, but not at the end of summer, which implies that hoverfly phenology is affected by a change in temperature, while carabid beetle abundance exhibited a delay in phenology in summer at higher altitudes. We suggest that species that are expected to be most affected by climate change, such as ectotherms and species with poor dispersal ability should be prioritised as the best indicators for monitoring and conservation management purposes.

Keywords

climate change; Carabidae; Syrphidae; Aves; altitudinal gradient; species assemblage

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Introduction

Climate change has a dramatic effect on the geographical ranges of many plant and animal species (Parmesan et al. 1999; Hill et al. 2002; Wilson et al. 2007; Wilson and Maclean 2011). Not only are species ranges expanding or moving northwards, they are also shifting to higher altitudes (Konvicka et al. 2003; Wilson et al. 2007). Furthermore, there is evidence of phenological change in insect species earlier in the season (Stefanescu et al. 2003), which is because growth rate is directly related to temperature (Bale et al. 2002). There is increasing knowledge about the effect of climate change on different species groups over latitudinal (Chen et al. 2011; Devictor et al. 2012), as well as altitudinal gradients (Hill et al. 2002; Chen et al. 2009; Pizzolotto et al. 2014; McGrann and Furnas 2016).

Altitudinal gradients can be used as a model for future impacts of increasing temperatures on biodiversity (Botes et al. 2006; Korner 2007). Many patterns of biodiversity are dependent on altitude, with the gradual decreasing and the hump-shaped relationships being the most commonly described (Rahbek 1995; Hodkinson 2005; Sanders and Rahbek 2012). Some of the underlying mechanisms for these patterns are source-sink dynamics (Kessler et al. 2011), geometric constraints (Rahbek 1995; Romdal and Grytnes 2007), disturbance (Bunn et al. 2010), evolutionary history (Machac et al. 2011), climate and productivity (Rahbek 1995; Wang et al. 2009) and species physiology (Žagar et al. 2018). A general negative metabolic response to temperature shifts was observed for high elevation specialists across vertebrate and invertebrate ectotherm taxa (Žagar et al. 2018). However, only a few abiotic parameters change gradually with altitude: atmospheric pressure, temperature and clear sky turbidity (Korner 2007). If the change is only measured in one habitat type, the direct effect of environmental temperature on animals can be determined (Bale et al. 2002; Tylianakis et al. 2008). Therefore, it is important to eliminate habitat change as a factor and take into account only the change in biodiversity across an altitudinal gradient in more or less homogenous and more or less non-fragmented habitat.

Although many different organisms have already been investigated for altitudinal distribution (Hodkinson 2005; Sanders and Rahbek 2012), they were all investigated in different habitats and regions (Sanders and Rahbek 2012). In butterflies, it was found that, due to climate change, the high altitude species and northern latitudinal species were going upwards to higher altitudes or latitudes (Wilson et al. 2007). Thus, the phenological window which was narrower on higher altitude may increase with climate change, because of warmer temperatures (Illán et al. 2012). Only a few studies have, however, considered species groups with different traits when studying biodiversity structure across an altitudinal gradient in the same habitat.

In this study, we investigated the influence of altitude and season on patterns of alpha and beta diversity and abundance of carabid beetles (Coleoptera: Carabidae)

and hoverflies (Diptera: Syrphidae) as ectotherms and passerine birds (Aves: Passeriformes) as endotherms in a mixed Dinaric beech and fir forest (*Omphalodo-Fagetum* s. lat.) in Central Europe. All of these groups are known to be good indicators for environmental and climate change (Furness and Greenwood 1993; Sommaggio 1999; Kotze et al. 2011; Pizzolotto et al. 2014). However, selected groups are very different in their mobile capabilities with forest species of carabid beetles being predominantly wingless with low dispersal power (Kotze and O'Hara 2003; Pizzolotto et al. 2016) and thus highly dependent on habitat connectivity (Jopp and Reuter 2005). It is well known that carabid beetle assemblages change rapidly due to environmental changes (Gobbi et al. 2015; Prass et al. 2017). We considered carabid beetles, which include high trophic species variability from predators, herbivores to omnivores (Lövei and Sunderland 1996), as a model group for low dispersal mode. As a model group for medium dispersal mode, we have selected hoverflies with all species in the assemblage having wings and being higher dispersers than carabid beetles, some species even being partly migratory (Odermatt et al. 2017). The hoverflies, as adult pollinators and as larvae, occupy a large radiation of niches, varying from plant feeding, predators, microbe feeders or saproxylic species. In many studies, they are shown to be sensitive to habitat disturbance in agricultural land, as well as forest landscapes (Sommaggio 1999; Gittings et al. 2006; Schweiger et al. 2007; Smith et al. 2009; de Groot et al. 2016). Passerine birds are known as the most mobile species group and were selected in our study as a model group for high dispersal mode. According to their good flight capabilities, the birds are able to exhibit longer distance seasonal flights and dispersal from few to some thousands of kilometres, shown to largely depend on their habitat specialism (Martin and Fahrig 2018). The forest assemblages of passerine birds mainly contain insectivore and granivore species (Snow and Perrins 1998).

First, we looked at the possible influence of temperature by comparing differences in diversity patterns between higher and lower altitudes, according to taxonomic groups in continuous non-fragmented forest area, to avoid the effects of habitat fragmentation. We then examined differences in the phenology of ectotherm insect groups with respect to altitude. The studied species groups can be differentiated on the basis of thermoregulation, mobility and degree of specialism. First, we expected ectotherms (carabid beetles, hoverflies) to exhibit greater dissimilarity across an altitudinal gradient than endotherms (birds), since the former is more affected by temperature during their life cycle (Žagar et al. 2018). Secondly, it is expected that species groups with greater dispersal ability, such as hoverflies, will exhibit a smaller change in assemblages than less mobile species, such as flightless carabid beetles (Steinitz et al. 2006). Thirdly hoverflies, which have high metabolic cost compared to flightless carabid beetles (Harrison and Roberts 2000), exhibit different phenology patterns across an altitudinal gradient because they are more dependent on temperature (Gilbert 1984).

Materials and methods

Area description

To study climate driven effects across an elevational gradient, we selected a continuous and non-fragmented forest area of Mt. Krim (45°58'N, 14°25'E), 10 km south of Ljubljana (central Slovenia), which is part of a continuous montane forest range, extending from Slovenia across the western Balkan Peninsula to Serbia. The area is 140 km^2, 77% of which is covered with forest and 20% of which is not forested, the remainder being urban areas (i.e. settlements) which are situated only in the lowlands. Mt. Krim is a medium altitudinal mountain in the North Dinaric Alps ranging from 290 to 1108 m a.s.l. The slopes are covered predominantly with mixed temperate forest of *Omphalodo-Fagetum* s. lat. in which beech (*Fagus sylvatica*) is the dominant tree species (36%). Other common tree species are silver fir (*Abies alba*) and Norway spruce (*Picea alba*). Most of the forest is in an old growth phase, with trees whose trunk diameters are more than 30 cm at breast height. Clearings are small and dispersed, mostly around the settlements (Vrezec 2003; Vrezec and Tome 2004). During the study, Mt Krim was studied on three altitudinal belts (low (300–550 m), middle (550–800 m) and high (800–1100 m). The sampling sites in altitudinal belts were chosen to avoid larger forest clearings and in such a way that they did not differ in type, age, tree species composition, including tree density/abundance, light and other environmental conditions and forest structure.

Survey protocol

Fieldwork was conducted in spring, summer and autumn of 2010. During this survey, the altitudinal distribution of three species groups was investigated: carabid beetles, hoverflies and passerine birds. These groups were investigated in the three altitudinal belts.

The carabid beetles were sampled with pitfall traps using vinegar as an attractant (Vrezec and Kapla 2007). A line of five traps at 20 m spacing was set in each altitudinal belt. The traps were set every month for five to seven days in April (19.4–26.4), May (15.5–21.5), June (18.6–23.6), July (21.7–28.7), August/September (28.8–4.9) and October (1.10–8.10). All carabid beetles were collected and identified in the laboratory using determination keys (Mueller 1931; Müller-Motzfeld 2006).

The hoverfly assemblage was assessed using transect counts and malaise traps (Leather 2005). Ten transects of 100 m were established in each altitudinal belt. Transect counts were conducted at the beginning of June, July and August, only on sunny days. Malaise traps were set from 15 April to 31 October in each altitudinal belt. Each trap was filled with alcohol and emptied every 13 to 16 days, 13 times. Although the traps were not replicated per altitudinal belt, it gives an indication of the phenological dynamics. The transects were positioned in areas with mixed deciduous/coniferous forest. All specimens were collected and identified in the laboratory, according to Van Veen (2004).

The passerine birds were counted at 16 points (Bibby et al. 2000). Four points were established in the low, six in the middle and six in the high altitudinal belt. Two counts were conducted: one in March/April and one in April/May. The counts were carried out during the morning hours between 5:00 a.m. and 10:00 a.m. on clear and sunny days. Every count session on the point took 5 minutes. Only forest birds which showed territorial singing behaviour were taken into account (Bibby et al. 2000).

The temperature was measured with a temperature logger (LogTag Trix–8 Temperature Recorder, accuracy ± 0.5 °C). In each altitudinal belt, a logger was placed on the tree. The temperature was measured every six hours during the sample period.

Statistical analysis

Species assemblage, species richness and abundance per group per altitudinal belt were calculated. Data on carabid beetles and hoverflies were repeated over time and pooled for each altitudinal belt per transect for the hoverflies or trap for the carabid beetles. The relative number of animals/species per day or per 15 days was calculated for the carabid beetles and the hoverflies, respectively. In bird surveys, the maximal abundance from two counts was taken into consideration and expressed as number of territorial birds per point. A permutational MANOVA (PerMANOVA) with the Jaccard dissimilarity index was used to test the differences in species assemblages between the altitudinal belts using only the transect data (Anderson 2001). As a post hoc test, every belt was compared with the other belts using the PerMANOVA and then corrected with the Holm correction (Holm 1979). The results of the PerMANOVA were visualised with NMDS. The species replacement (Simpson similarity index) and the dissimilarity derived from nestedness in the Jaccard dissimilarity index were calculated (Baselga 2012). A rarefaction curve was prepared for every group and altitudinal belt to check whether the sampling effort was sufficient. The species-sample-based R/E curve and sample completeness curve were prepared. The differences in species richness and abundance between altitudinal belts were analysed with a Generalised Linear Model (GLM) using Poisson error distribution (McCullagh and Nelder 1989) using only the data of the transects.

The following traits were investigated: food type (hoverflies: predator, microphagous and phytophagous; birds: seeds and invertebrates), wing length and the body length of the animal. The wing length indicated the dispersal possibility as large animals with large wings having higher dispersal possibility (Delettre 1988). For the same reason, the body length was taken into account, as large animals (also non-flying animals) have a greater dispersal potential than small animals. The data on the different traits per species were extracted from the literature (Snow and Perrins 1998; Müller-Motzfeld 2006; Reemer et al. 2009; Speight 2017) or measured with the animals which were caught. The dissimilarity in traits between the different altitudinal belts was calculated with Fourth Corner Analysis using the Jaccard index (Legendre et al. 1997; Dray and Legendre 2008). For these simulations, model 1 was used, which permutates the values within each column (species) (Dray and Legendre 2008). Each group was investigated separately.

For the seasonal dynamics, the repeated data-sets of the carabid beetles and hoverflies (only malaise trap data) were used. We were only interested in the seasonal dynamics and not differences in abundance between altitudes. Therefore, the species richness and relative abundance data per period were transformed into a percentage of the total number of species/individuals per altitudinal belt.

All analyses were done with the statistics programme R (R Development Core Team 2011). For the PerMANOVA, the "adonis" function in the "vegan" package (Oksanen et al. 2013) was used. For the Fourth Corner Analysis, the "fourthcorner" function of the "ade4" package (Dray and Dufour 2007) and for the rarefaction the package "iNEXT" (Hsieh et al. 2019) were used.

Results

There was a gradual decrease in average temperature from low to the highest altitude (Table 1: $F_{2, 2855} = 63.672$, $P < 0.001$). All altitudes were significantly different from each other (low vs. middle: $P < 0.001$; middle vs. high: $P < 0.001$, low vs. high: $P < 0.001$). On average, there was a difference of approximately 3 °C between the lowest part on the north side and the top. It is interesting that the minimum temperature has a larger difference between altitude than the maximum temperature. The measured temperature between March and November in 2010 was a minimum of -4.7 °C and maximum of 32.1 °C in the lowest part and minimum -10.7 °C and maximum 31.1 °C on the top of Mt. Krim. However, these temperatures were only measured at one place on each altitudinal belt.

In total, 18 carabid species where found (Appendix 1). After rarefaction of the species diversity, it was found that almost all species were detected in carabid beetles; proportion of 0.9501 (lower altitude), 0.9927 (middle altitude) and 0.9845 (higher altitude) of detected species (Fig. 1). Carabid beetle assemblages differed across the altitudinal gradient (Fig. 2a: pseudo $F = 3.08$, $P < 0.01$). Almost 34% of the data was explained by the difference in altitude ($R^2 = 0.339$). All altitudes were significantly different from each other (low-middle: $F = 3.23$, $P < 0.05$; middle-high: $F = 3.52$, $P < 0.05$; low-high: $F = 3.96$, $P < 0.01$). Only the species turnover showed a significant difference between different altitudinal belts (Table 2). The number of species in the high altitudinal belt was not different from the other altitudinal belts (Fig. 3a: low: $Z = 1.953$, $P =$ ns; middle: $Z = 1.834$, $P =$ ns). However, the abundance was lower in the high altitudinal belt than the lower belts (Fig. 3b: low: $Z = 4.354$, $P < 0.001$; middle: $Z = 3.160$, $P < 0.01$). Regarding the seasonal

Table 1. Differences in temperature parameters (in °C) between altitudes in the period from March to November 2010.

Altitude	Mean	SD	Min	Max
low	13.17	6.40	-4.70	30.90
middle	11.60	6.46	-7.60	30.60
high	9.85	6.78	-10.70	31.00

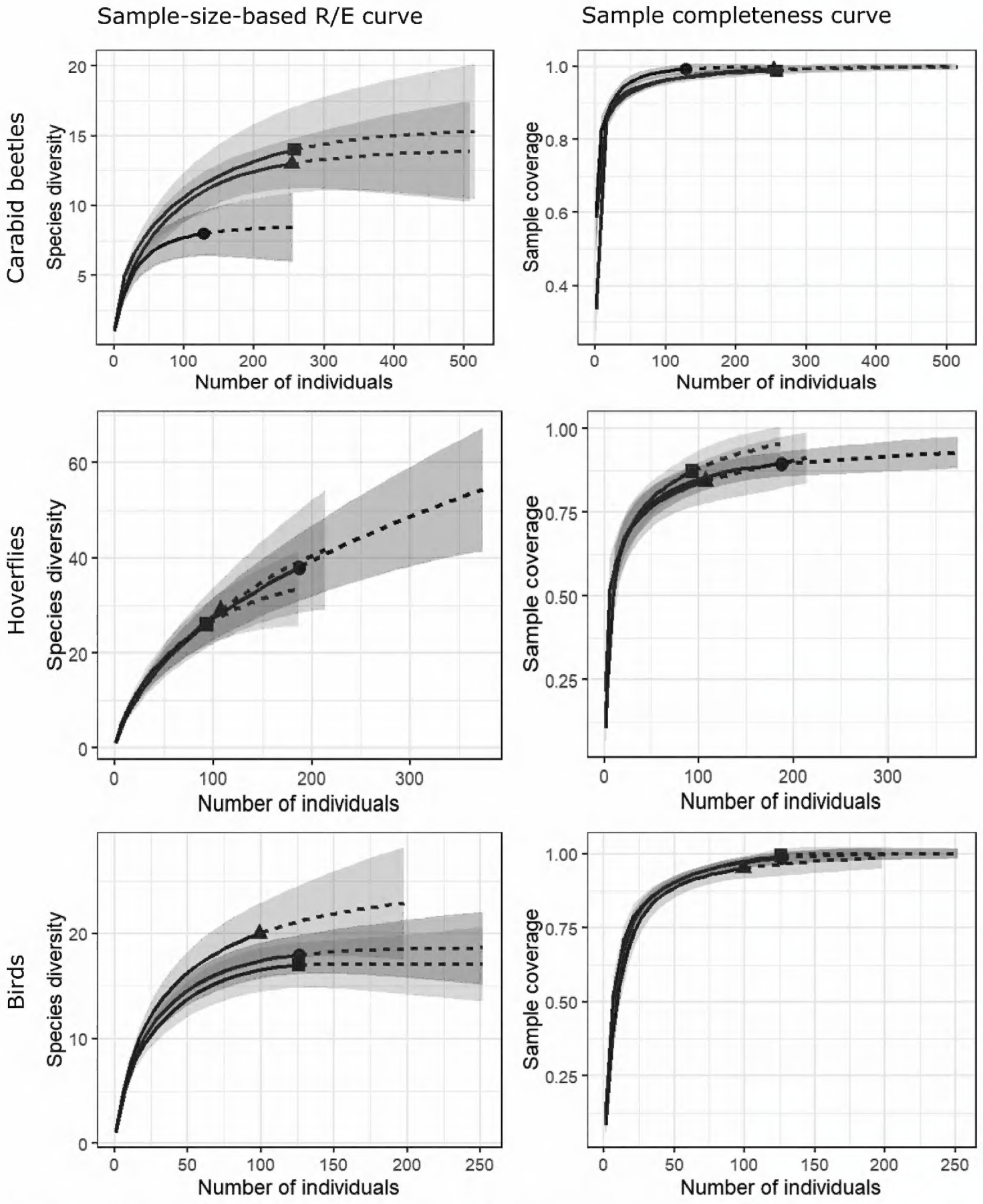

Figure 1. The rarefaction of carabid beetle, hoverfly and bird species richness for different altitudes. For each species group, the species-sample-based R/E curve and sample completeness curve is shown. The triangle shows the diversity in the lower belt, the quadrant shows the diversity in the middle belt and the circle shows the diversity in the highest belt.

dynamics of the carabid beetles, it was found that the summer peak in abundance was later at higher altitudes than lower altitudes (Fig. 4a), while the summer peak in number of species was the same for all altitudes (Fig. 4b). Furthermore, there was a change in

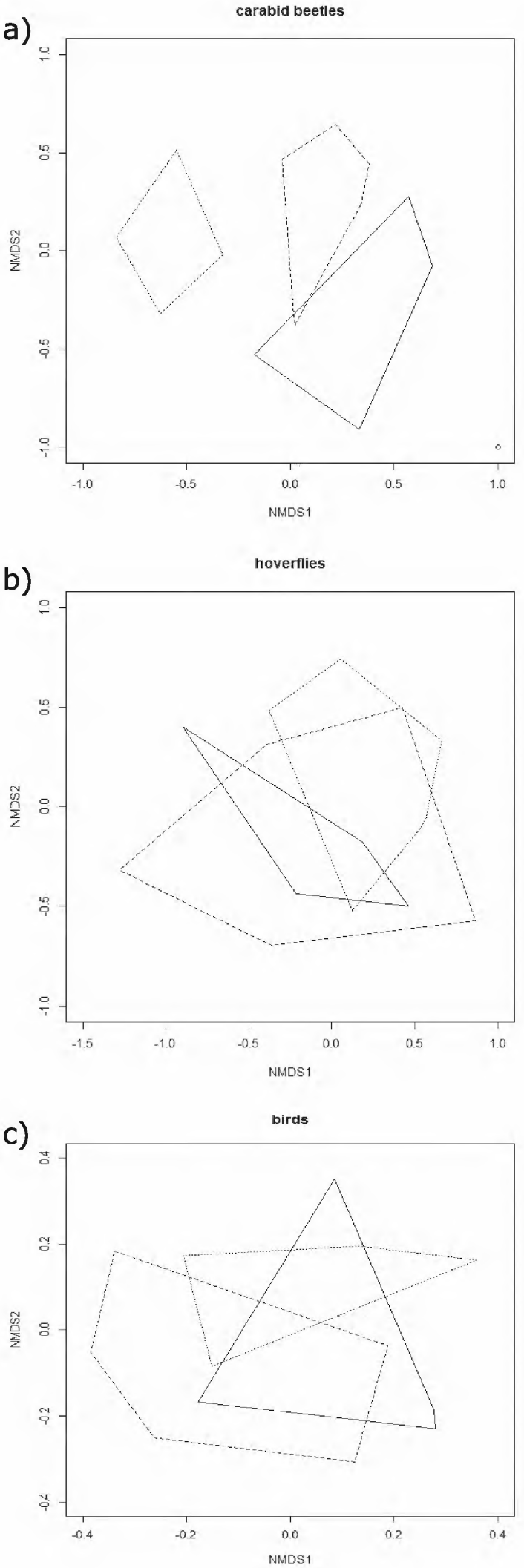

Figure 2. NMDS plots showing the differences in assemblages between altitudinal belts for **a** carabid beetles **b** hoverflies and **c** passerine birds. The stippled line indicates the low altitudinal belt, the dashed line indicates the middle altitudinal belt and the black line indicates the high altitudinal belt.

Table 2. Beta diversity partition into species turnover and nestedness across the altitudinal gradient. The Jaccard dissimilarity index is used. Statistically significant differences marked in bold ($P < 0.05$).

Species groups	Jaccard dissimilarity index			Species turnover			Nestedness		
	F	R^2	*P*	*F*	R^2	*P*	*F*	R^2	*P*
Carabid beetles	**3.081**	**0.339**	**0.001**	**4.204**	**0.412**	**0.004**	0.460	0.071	0.647
Hoverflies	**2.108**	**0.140**	**0.001**	**2.510**	**0.162**	**0.005**	-0.273	-0.266	0.987
Birds	1.612	0.199	0.126	1.398	0.177	0.260	2.3786	0.268	0.179

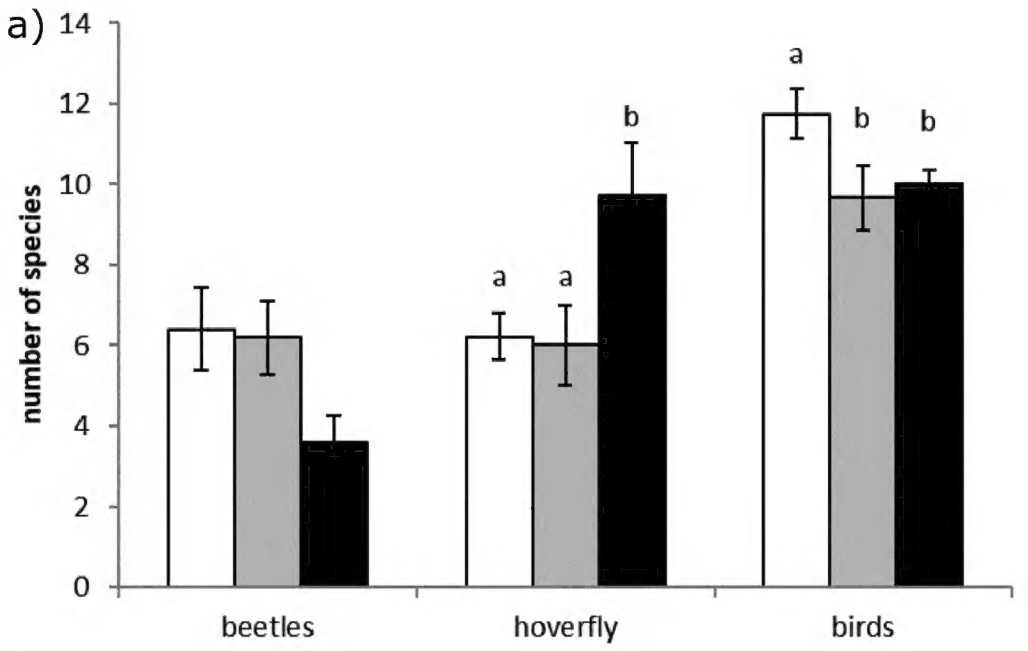

Figure 3. Differences in **a** the number of species and **b** the abundance of beetles, hoverflies and birds across the altitudinal belts from the lowest (white bar) to the highest belt (black bar). Different letters indicate significantly different groups within one species group.

body size from lower to higher altitudes (Table 3). At the low altitude were species with larger body size (average = 19.6 mm), while in the middle altitudinal belt, carabids were smaller than those in the lower belt (16.1 mm). In the higher altitudinal belt, there were larger species on average (average 21.2 mm). All the species were carnivorous and wingless; therefore, analysis was not possible for the traits of wing length and feeding mode.

In total, 88 species of hoverflies were found, 61 species were found on the transects and 46 species with the malaise trap (Appendix 2). After rarefaction of the species di-

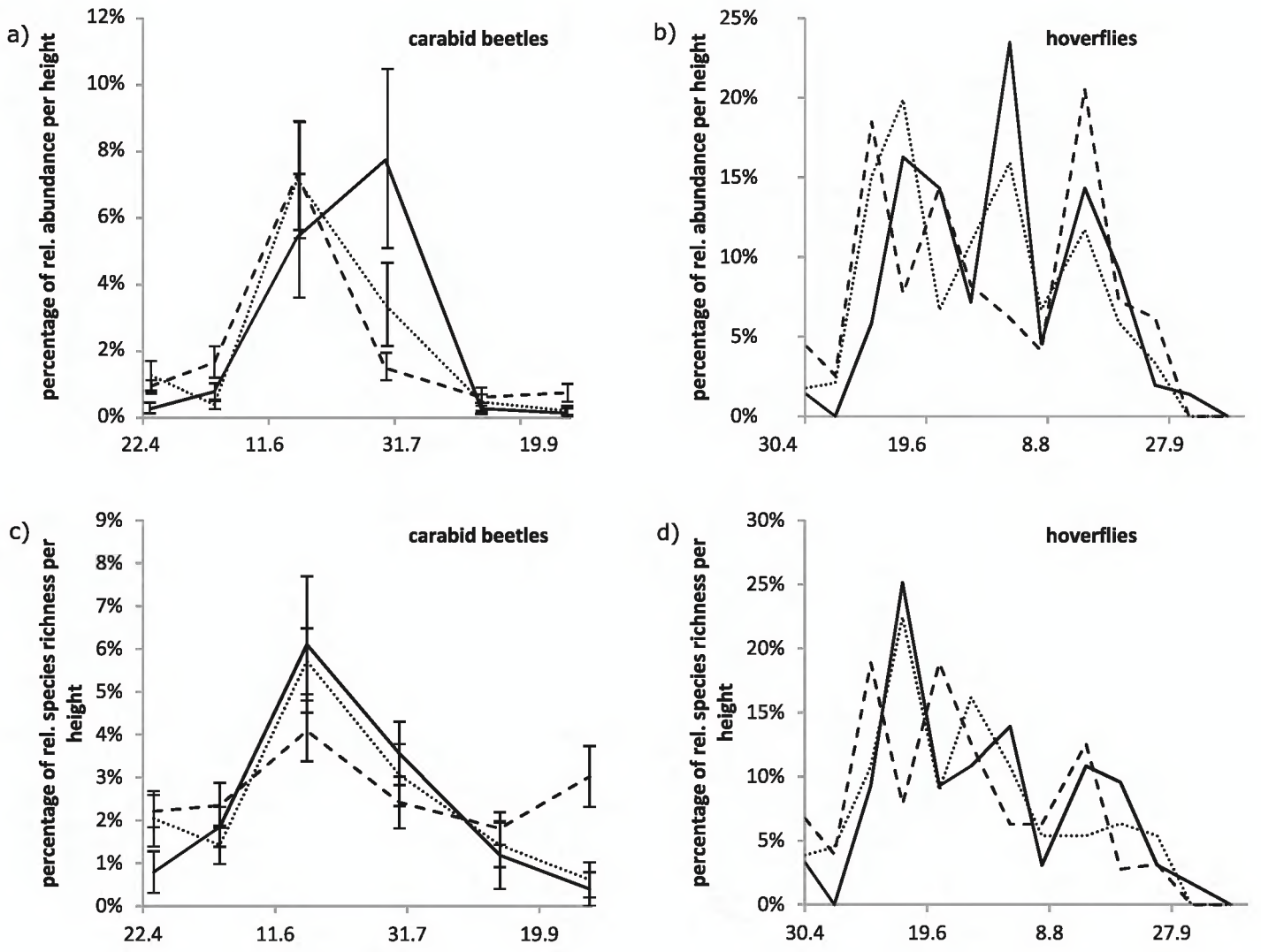

Figure 4. Seasonal dynamics of the number of species and abundance of carabid beetles and hoverflies at three different altitudes (485 m, 800 m and 1054 m a.s.l.). The stippled line indicates the low altitudinal belt, the dashed line indicates the middle altitudinal belt and the black line indicates the high altitudinal belt.

Table 3. Differences in the traits of the assemblages of passerine birds, carabid beetles and hoverflies between the different altitudinal belts. * no variability in trait parameter within group species was found.

Group	Trait parameter	Stat.	Value	*P*
Carabid beetles	Diet*			
	Body size	F	2.83	0.02
	Wing length*			
Hoverflies	Diet	χ^2	4.86	0.21
	Body size	F	1.19	0.25
	Wing length	F	0.67	0.47
Passerine birds	Diet	χ^2	0.29	0.65
	Body size	F	1.60	0.03
	Wing length	F	1.93	0.02

versity of the transects, it was found that almost all species were detected in hoverflies (proportion of 0.84 (lower altitude), 0.87 (middle altitude) and 0.89 (higher altitude) of detected species; Fig. 1). There were significant differences in hoverfly assemblages between the altitudinal belts (Fig. 2b: pseudo $F = 2.11$, $P < 0.001$). Only around 17%

of the data was explained by altitude (R^2 = 0.14). There was almost no overlap in assemblages between the high and low belt (pseudo F = 2.43, P < 0.001), but the assemblage in the middle belt largely overlapped with that in the low and the high belts, although it was still significantly different (low-middle: pseudo F = 2.24, P < 0.01; middle-high: pseudo F = 1.69, P < 0.05). Only the species turnover showed a significant difference between the different altitudinal belts (Table 2). The number of species was highest in the high altitudinal belt compared to the lower altitudes (Fig. 3a: low: Z = -2.839, P < 0.01; middle: Z = -3.361, P < 0.001). Additionally, the abundance was highest in the high altitudinal belt compared to the lower belts (Fig. 3b: low: Z = -6.821, P < 0.001; middle: Z = -7.003, P < 0.001). There was a difference between the altitudinal belts in the number of species and the abundance (species: X^2 = 10.582, P < 0.001; abundance: X^2 = 13.558, P < 0.001). In both cases, there was a difference between the low altitudinal belt and the other two belts and no difference between the middle and high altitudinal belts. There were strong phenological differences in hoverflies for the different altitudinal belts (Fig. 4c, d). There were three peaks of hoverfly abundance. In the first two peaks, the peak in the low altitude belt was earlier than those in the middle and high altitudinal belts (Fig. 4c). The last abundance peak was in the same period in all altitudinal belts. The same pattern was found for the seasonal dynamics in species numbers (Fig. 4d). Abundance was highest in July and August, while the highest number of species was found in June. There was no difference in trait composition between the different altitudinal belts for the hoverflies (Table 3).

In total, 24 passerine bird species were recorded (Appendix 3). After rarefaction of the species diversity, it was found that almost all species were detected in birds (proportion of 0.9922 (lower altitude), 0.9885 (middle altitude) and 0.9923 (higher altitude) of detected species (Fig. 1). The bird assemblage was not significantly different between the altitudinal belts (Fig. 3c: pseudo F = 1.61, P = ns). A total of 20% of the data was explained by altitude (R^2 = 0.199). Species turnover and nestedness were not different for the different altitudinal belts (Table 2). The species number did not differ between the altitudinal belts, but was lower in the high altitudinal belt (Fig. 4a: low-middle: Z = -1.087, P = ns; low-high: Z = -1.525, P = ns). However, the number of species decreased gradually across the altitudinal gradient (Z = -1.985, P < 0.05). There was no difference between the low and the middle belts in terms of abundance (Fig. 4b: low-middle: Z = -1.397, P = ns), but there was a difference between the low and high altitudinal belts (Fig. 4a: low-middle: Z = -2.205, P < 0.05). Abundance gradually decreased with increasing altitude (Z = -2.462, P < 0.05). There was a change in trait composition over the different belts for body size, measured as weight and wing length (Table 3), but the trait average did not show a trend with altitudinal gradient.

Discussion

Patterns in assemblage structures for different species groups varied over the altitudinal gradient of non-fragmented montane forest area. The bird assemblage did not differ

with respect to altitude, whereas both insect groups did. Furthermore, the carabid beetle assemblage differed more with increasing altitude than that of the hoverflies. The effects of altitude on species richness and abundance between the species groups were contrasting. In both birds and carabid beetles, the abundance and number of species decreased with increasing altitude, while in the hoverfly assemblage, abundance and the number of species increased. Regarding phenology, the hoverflies showed distinct delays in abundance and species number peaks for higher altitudes in spring and early summer, while in late summer, the peaks were in the same period. Only carabid abundance showed a delay at higher altitudes, whereas the species richness peak occurred at the same time for all altitudes.

Altitudinal differences in assemblages

The first question raised was whether the discovered altitudinal patterns are caused by factors other than temperature (McCain 2009). The patterns were not due to the area (Rahbek 1997) and sampling effect (Colwell and Coddington 1994) because the study design was standardised in sampling efforts. Static evolutionary models predict that, at lower altitudes, there is more migration, which also results in higher diversity, while at higher altitudes, there is less dispersion and, thus, a higher extinction rate and lower diversity (Lomolino 2001). Due to the geographical and landscape characteristics of our study area, we were able to rule out several parameters that could contribute to the differentiation of the studied assemblages. First, the area is part of a large continuous non-fragmented forest area in the Northern Dinaric Alps in southern Slovenia, which extends further south to Croatia, so dispersion of forest species is not limited by habitat fragmentation and the extinction risk is therefore low. Secondly, the species found in the assemblages are not isolated relict populations and are distributed widely in the Dinaric Alps and beyond. Thirdly, due to the relatively short distances between sampling sites in the different altitudinal belts (< 3 km), all sites experienced similar weather conditions, especially with respect to precipitation. The patterns are in accordance with the gradient proposed by McCain (2009) and, therefore, it can be assumed that the gradient found here is driven mainly by altitudinal temperature differences.

The contrasting seasonal activity, richness and assemblage patterns observed during this study could be due to the different traits of the investigated species groups. First, the strong difference between the birds and the insect groups could be explained by differences in thermoregulation (Miller and Harley 2009). Insects are ectotherms and are dependent on the environmental temperature for development (Bale et al. 2002). In the case of the carabid beetles, there was a decrease in the number of species and abundance across a temperature gradient. In addition, insects are strongly partitioned in niches on the basis of temperature (Boggs and Inouye 2012). This means that some species are adapted to colder, higher elevation areas and some to warmer, lower elevation areas (Žagar et al. 2018). This is reflected in the strong species turnover observed in both carabid beetles and hoverflies. Birds, on the other hand, did not show any dif-

ferences in species assemblages between the different altitudinal belts. Endotherms are better adapted to different climates and only exhibit a turnover on a larger scale (Buckley and Jetz 2008). In addition, birds are extremely mobile species and almost half of the recorded species are migratory or at least partly migratory and do not overwinter at their breeding sites. The observed decrease in abundance can only be an indirect effect of temperature. Lepidoptera larvae are an important food source for the observed passerine species (Barbaro and Battisti 2011). As lepidopteran larvae are influenced by temperature, food availability might be lower at higher altitudes, which in turn affects abundances (Randall 1982; Bears et al. 2009), although this is not the case for some other insect groups (de Groot and Kogoj 2015, this study).

The dispersal ability or mobility of a species is another aspect which could result in differences in species assemblages (Hubbell 2001). This could explain the difference in assemblage patterns between the studied insect groups (the brachypterous carabid beetles and macropterous hoverflies). The non-flying carabids had a distinct assemblage for each altitude. Forest carabid beetles in our study were all brachypterous and therefore they disperse on the ground within smaller distances and have consequently smaller ranges (Kotze and O'Hara 2003; Jopp and Reuter 2005; Pizzolotto et al. 2016). Hoverflies, on the other hand, exhibited an overlap in altitudinal ranges, with the assemblages of the low and the high altitudes overlapping slightly and the assemblages of the mid altitudinal belt overlapping to a large extent with those of both the low and the high altitudinal belts. Hoverflies can fly several kilometres and some species are even migratory (Rotheray and Gilbert 2011). Therefore, they can spread over large areas relatively faster than flightless carabids. Given this, we suggest that altitude has a greater effect on the turnover of less mobile than mobile species.

On the other hand, the abundance and species richness of the hoverflies increased with altitude in forested areas. One of the reasons could be that there is competition with hymenopteran species for food resources. It was observed that, towards the north, a higher percentage of plants are pollinated by flies, because bees have their optimum at higher temperatures (Rotheray and Gilbert 2011). The abundance of Diptera species (e.g. *Cheilosia fasciata*), was found to be even negatively correlated with temperature (de Groot and Kogoj 2015), which might also be the case in other syrphid or other dipteran species (Miličić et al. 2018). Competitive relationship between hymenopteran and dipteran pollinators and even predators should, however, be explored more.

Altitudinal differences in phenology

As predicted, the carabid beetles and hoverflies exhibited different patterns of activity over the season. The phenology of hoverflies was strongly correlated with the weather. The earlier flying species showed a delay in flying with increasing altitude, which was also observed with butterflies (Illán et al. 2012). Flying in hoverflies takes a large amount of energy and mainly occurs on sunny days, when they fly in large

numbers (Gilbert 1984; Gilbert 1985). The altitudinal difference in temperature was much higher in spring than in summer. This would, therefore, also influence the abundance and the species richness more strongly for hoverflies. The flightless carabid beetles showed a more stable pattern, where there was no altitudinal difference in species richness, while activity was dependent on the temperature. Additionally, carabid beetles showed a higher species turnover towards higher altitudes, which means a higher proportion of high elevation and cold adapted specialists in the carabid assemblage compared to the hoverfly assemblage. This could contribute to greater differences in phenological response across altitude in the more generalist hoverflies than in the more specialised carabids.

Altitude and climate change

Altitudinal patterns can be used to predict future patterns in a continuous habitat under the influence of climate change (Botes et al. 2006; Korner 2007; Illán et al. 2012). We found that endotherms and more mobile species had a smaller turnover than ectotherms and less mobile species, from which we can predict that the former species will undergo a less extreme shift than the latter. This was indeed found in birds, which showed no shift (Chen et al. 2011), but in butterflies, there was a strong shift, which could amount to a maximum of 100 m in 50 years (Konvicka et al. 2003; Wilson et al. 2007) or a median speed of 11 m per year (Chen et al. 2011) and for hoverflies, there was a shift predicted for several species (Miličić et al. 2018). On a latitudinal gradient, it was found that many species' ranges move northwards (Parmesan et al. 1999); however, birds have a smaller climate debt than butterflies (Devictor et al. 2012). Across a latitudinal range, the connectivity between habitats plays a very important role in species' response to climate change (Settele et al. 2008). In connected and non-fragmented natural habitats, such as temperate forests with a small altitudinal range, temperature affected insects more than birds. Therefore, it is expected that, over small ranges, birds will be less affected by climate change than insects, such as hoverflies and carabid beetles.

The results of study were constrained in time and space, as the sampling only occurred for one year and only on one mountain. As pointed out, the dynamics of the species groups can be heavily affected by the temperature and this could give different results for the different years. However, because the different belts were relatively close to each other, large annual differences would be equally impacting all the different altitudinal belts. In addition, the different belts of Mt. Krim were sampled with more transects, point counts or traps. However, this case study confirmed expected temperature driven mechanisms in assemblage changes. It is therefore important to note for future studies that additional mountains should be sampled in the same way for more years.

When examining altitudinal shifts in patterns, it is important to consider that climate change will affect different functional groups with different traits in different

ways. Species that are expected to be most affected by climate change, such as ectotherms and species with poor dispersal ability, should be prioritised, as they are the best indicators for monitoring and conservation management purposes. Current monitoring and conservation programmes are mainly focused on large and charismatic species (e.g. large mammals and birds), which are usually at the top of the food chain in the ecosystem (Pereira and David Cooper 2006), but are, at least with respect to climate change, less affected and, consequently, less threatened and might not be appropriate indicators for climate-driven ecosystem changes.

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Appendix 1

Carabid beetle (Carabidae) species which were found per altitudinal belt. The number of individuals per 5 trap nights per altitudinal belt is shown.

Altitudinal belt	Low			Middle			High		
Species	Average	Min	Max	Average	Min	Max	Average	Min	Max
Abax carinatus	0.2	0	1	0	0	0	0	0	0
Abax ovalis	1.8	1	2	0.2	0	1	0	0	0
Abax parallelepipedus	0.4	0	1	0.2	0	1	0.6	0	1
Abax parallelus	0.6	0	2	0.8	0	2	0	0	0
Aptinus bombarda	3.4	3	4	1.8	1	2	1.6	0	2
Carabus caelatus	0.2	0	1	0	0	0	0	0	0
Carabus catenulatus	1.6	0	3	0	0	0	0.4	0	1
Carabus coriaceus	1	0	3	0.6	0	1	0.4	0	2
Carabus creutzeri	0	0	0	0	0	0	0.2	0	1
Cychrus attenuatus	0.6	0	2	0	0	0	0	0	0
Licinus hoffmannseggi	0	0	0	0.2	0	1	0	0	0
Molops ovipennis	0.2	0	1	0.4	0	1	0	0	0
Molops piceus	0.6	0	1	0.6	0	1	0	0	0
Molops striolatus	0.4	0	1	1.2	0	4	0.2	0	1
Nebria dahli	0	0	0	1.2	0	2	0.4	0	1
Pterostichus burmeisteri	0	0	0	2.4	0	4	1	0	2
Pterostichus transversalis	0.4	0	1	0	0	0	0	0	0
Trechus sp.	0	0	0	0.2	0	1	0	0	0

Appendix 2

Average, minimum and maximum of hoverfly (Syrphidae) species abundance which were found per altitudinal belt for the transects and malaise traps.

Method	Transect									Trap		
Altitudinal Belt	Low			Middle			High			Low	Middle	High
Species	Average	Min	Max	Average	Min	Max	Average	Min	Max			
Baccha elongata	0.2	0	1	0.1	0	1	0.3	0	1	1	1	0
Brachypalpoides lentus	0	0	0	0.1	0	1	0	0	0	1	0	0
Brachypalpus laphriformis	0	0	0	0	0	0	0	0	0	1	1	0
Caliprobola speciosa	0	0	0	0	0	0	0	0	0	3	0	0
Callicera aenea	0	0	0	0	0	0	0	0	0	0	0	1
Chamaesyrphus scaevoides	0	0	0	0	0	0	0.1	0	1	0	0	0
Cheilosia antiqua	0	0	0	0.1	0	1	0	0	0	0	0	0
Cheilosia chloris	0	0	0	0	0	0	0	0	0	0	1	0
Cheilosia himantopa	0	0	0	0.1	0	1	0.1	0	1	0	0	0
Cheilosia impressa	0	0	0	0.1	0	1	0	0	0	0	0	0
Cheilosia lasiopa	0.1	0	1	0	0	0	0.1	0	1	0	0	0
Cheilosia melanopa	0	0	0	0	0	0	0.1	0	1	0	0	0
Cheilosia pagana	0.1	0	1	0	0	0	0.1	0	1	0	0	0
Cheilosia personata	0	0	0	0	0	0	0	0	0	0	0	1
Cheilosia scutellata	0.1	0	1	0	0	0	0.1	0	1	0	0	0
Cheilosia vulpina	0.2	0	1	0	0	0	0.3	0	1	0	0	0
Chrysostoxum lessonae	0	0	0	0	0	0	0	0	0	1	0	0
Chrysotoxum arcuatum	0	0	0	0	0	0	0	0	0	0	4	3
Chrysotoxum bicinctum	0	0	0	0	0	0	0	0	0	0	0	12
Chrysotoxum elegans	0	0	0	0	0	0	0	0	0	0	0	1
Chrysotoxum fasciolatum	0	0	0	0	0	0	0	0	0	1	0	7
Chrysotoxum festivum	0	0	0	0	0	0	0.1	0	1	2	1	0
Chrysotoxum intermedium	0.1	0	1	0	0	0	0	0	0	6	13	4
Chrysotoxum octomaculatum	0	0	0	0	0	0	0	0	0	0	11	6
Chrysotoxum vernale	0	0	0	0	0	0	0.1	0	1	1	1	0

Method	Transect									Trap		
Altitudinal Belt	Low			Middle			High			Low	Middle	High
Species	Average	Min	Max	Average	Min	Max	Average	Min	Max			
Chrystoxum arcuatum	0	0	0	0	0	0	0	0	0	0	0	1
Criorhina berberina	0	0	0	0	0	0	0	0	0	2	4	1
Criorhina floccosa	0	0	0	0	0	0	0	0	0	0	1	0
Dasysyrphus albostriatus	0	0	0	0	0	0	0.1	0	1	0	0	0
Dasysyrphus friuliensis	0	0	0	0	0	0	0	0	0	0	0	1
Dasysyrphus venustus	0	0	0	0	0	0	0.1	0	1	0	1	1
Didea fasciata	0	0	0	0	0	0	0	0	0	0	1	0
Epistrophe eligans	0.1	0	1	0	0	0	0	0	0	0	0	0
Epistrophe flava	0	0	0	0.1	0	1	0	0	0	0	0	0
Epistrophe grossulariae	0.1	0	1	0.1	0	1	0.2	0	1	0	0	0
Episyrphus balteatus	1	1	1	0.7	0	1	0.9	0	1	8	39	35
Eristalis interrupta	0	0	0	0	0	0	0.1	0	1	0	0	0
Eristalis pertinax	0	0	0	0	0	0	0.2	0	1	0	0	0
Eristalis similis	0	0	0	0.2	0	1	0. 6	0	1	0	0	0
Eristalis tenax	0.1	0	1	0.2	0	1	0.2	0	1	0	0	0
Eumerus amoenus	0.1	0	1	0	0	0	0	0	0	0	0	0
Eumerus flavitarsis	0	0	0	0	0	0	0	0	0	0	2	0
Eupeodes lapponicus	0	0	0	0.4	0	1	0.2	0	1	0	1	4
Eupeodes luniger	0	0	0	0	0	0	0	0	0	1	0	0
Melangyna cincta	0	0	0	0	0	0	0	0	0	0	2	1
Melangyna compositarum	0	0	0	0	0	0	0.1	0	1	0	0	0
Melangyna lasiophthalma	0	0	0	0	0	0	0	0	0	0	1	1
Melangyna umbellatarum	0	0	0	0	0	0	0	0	0	0	0	3
Melanostoma scalare	0	0	0	0	0	0	0.1	0	1	2	0	4
Meligramma cingulata	0	0	0	0	0	0	0	0	0	1	1	0
Meliscaeva auricollis	0.1	0	1	0	0	0	0	0	0	3	1	1
Meliscaeva cinctella	0.4	0	1	0.1	0	1	0. 8	0	1	11	17	36
Merodon cinereus	0	0	0	0.1	0	1	0	0	0	0	0	0
Merodon constans	0	0	0	0.2	0	1	0	0	0	0	0	0
Merodon equestris	0	0	0	0	0	0	0	0	0	0	0	1
Merodon equestris	0	0	0	0.4	0	1	0.1	0	1	0	0	0
Microdon devius	0.1	0	1	0	0	0	0	0	0	0	0	0
Myathropa florea	0	0	0	0	0	0	0	0	0	1	0	2
Myathropa florea	0.6	0	1	0.1	0	1	0.3	0	1	0	0	0
Paragus albifrons	0.1	0	1	0	0	0	0	0	0	0	0	0
Paragus haemorrhous	0.2	0	1	0	0	0	0	0	0	0	0	0
Paragus pechiolli	0.1	0	1	0	0	0	0	0	0	0	0	0
Parasyrphus lineolus	0	0	0	0	0	0	0.1	0	1	0	0	0
Parasyrphus macularis	0	0	0	0	0	0	0.1	0	1	0	1	1
Parasyrphus malinellus	0.1	0	1	0	0	0	0	0	0	0	0	0
Parasyrphus punctulatus	0	0	0	0	0	0	0	0	0	1	0	1
Pipiza bimaculata	0	0	0	0.1	0	1	0	0	0	0	0	0
Pipiza quadrimaculata	0	0	0	0	0	0	0.2	0	1	0	0	0
Pipizella bispina	0	0	0	0.3	0	1	0	0	0	0	0	0
Platycheirus albimanus	0.1	0	1	0.3	0	1	0.1	0	1	0	0	4
Platycheirus cf. scutatus	0	0	0	0	0	0	0.3	0	1	0	1	1
Scaeva pyrastri	0	0	0	0	0	0	0.1	0	1	0	0	0
Sphaerophoria sp.	0.1	0	1	0	0	0	0	0	0	0	0	0
Sphegina clunipes	0.2	0	1	0	0	0	0	0	0	0	0	0
Sphegina sibirica	0	0	0	0	0	0	0.3	0	1	0	0	0
Sphegina verecunda	0.1	0	1	0	0	0	0	0	0	0	0	0
Syritta pipiens	0	0	0	0	0	0	0.1	0	1	0	0	0
Syrphus ribesii	0.2	0	1	0.6	0	1	0. 9	0	1	0	2	9
Syrphus torvus	0	0	0	0.2	0	1	0.1	0	1	0	1	1
Syrphus vitripennis	0.1	0	1	0.3	0	1	0. 6	0	1	0	1	4
Temnostoma vespiforme	0.4	0	1	0.2	0	1	0	0	0	0	0	0
Volucella inanis	0	0	0	0.1	0	1	0	0	0	0	0	0
Volucella pellucens	0.5	0	1	0.2	0	1	0.3	0	1	0	1	0
Xanthogramma laetum	0	0	0	0	0	0	0	0	0	1	2	1
Xanthogramma pedissequum	0	0	0	0	0	0	0	0	0	0	1	0
Xylota segnis	0.2	0	1	0.1	0	1	0.1	0	1	0	0	0
Xylota sylvarum	0	0	0	0	0	0	0	0	0	0	1	1

Appendix 3

Passerine bird species (Aves, Passeriformes) per altitudinal belt. The average number, minimum and maximum of individuals per count point per altitudinal belt is shown.

Altitudinal belt	Low			Middle			High		
Species	**Average**	**Min**	**Max**	**Average**	**Min**	**Max**	**Average**	**Min**	**Max**
Anthus trivialis	0.25	0	1	0.00	0	0	0.50	0	1
Certhia familiaris	0.00	0	0	0.17	0	1	0.50	0	2
Chloris chloris	0.25	0	1	0.00	0	0	0.00	0	0
Coccothraustes coccothraustes	0.25	0	1	0.00	0	0	0.00	0	0
Erithacus rubecula	4.00	3	5	3.67	3	5	3.17	2	4
Fringilla coelebs	4.00	3	6	4.67	3	6	4.00	2	5
Garrulus glandarius	1.25	0	2	0.33	0	2	0.83	0	2
Lophophanes cristatus	0.50	0	1	0.50	0	2	0.17	0	1
Loxia curvirostra	0.00	0	0	0.00	0	0	0.17	0	1
Nucifraga caryocatactes	0.00	0	0	0.00	0	0	0.17	0	1
Oriolus oriolus	0.25	0	1	0.00	0	0	0.00	0	0
Parus major	1.75	1	3	0.67	0	2	0.33	0	1
Periparus ater	2.50	2	3	2.67	1	4	2.83	0	5
Phylloscopus collybita	1.50	1	2	0.83	0	2	1.17	1	2
Poecile palustris	0.75	0	1	0.33	0	1	0.50	0	1
Pyrrhula pyrrhula	0.00	0	0	0.33	0	2	0.00	0	0
Regulus ignicapilla	0.75	0	2	0.50	0	2	0.50	0	2
Regulus regulus	0.50	0	2	0.33	0	1	0.67	0	2
Sitta europaea	0.75	0	3	0.00	0	0	0.00	0	0
Sylvia atricapilla	2.00	1	3	2.50	2	3	2.17	1	4
Troglodytes troglodytes	0.50	0	1	1.00	0	2	0.00	0	0
Turdus merula	2.00	2	2	0.67	0	1	1.50	1	2
Turdus philomelos	0.75	0	1	1.50	1	2	1.33	1	2
Turdus viscivorus	0.25	0	1	0.33	0	1	0.33	0	1